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Under siege: Isolated tributaries are threatened by regionally impaired metacommunities

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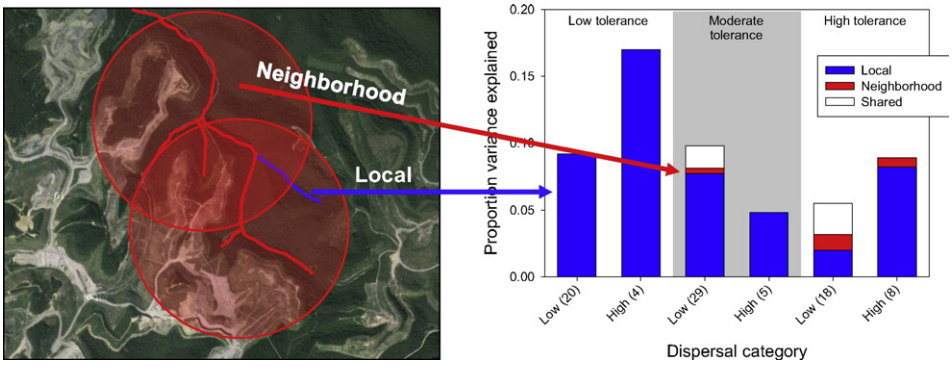
HIGHLIGHTS

- Isolation affects the ability of pristine streams to preserve regional biodiversity.
- Local condition explained the majority of variation in local communities.
- Isolation results in decreased mass and rescue effects of key low dispersing taxa.
- Increasing isolation also results in a regional proliferation of tolerant taxa.
- Protection of regional species' pools will require more than headwater conservation.

GRAPHICAL ABSTRACT



In heavily degraded regions, even the most pristine headwater streams are at risk due to the simultaneous decrease in mass and rescue effects of key low-dispersing taxa and proliferation of regionally dominant tolerant taxa.

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ABSTRACT

Pristine streams are often targeted as conservation priorities because of their ability to preserve regional biodiversity. However, isolation within heavily degraded regions likely alters important metapopulation and metacommunity processes (e.g., rescue and mass effects), affecting the ability of in-tact communities to boost regional conditions. To test this hypothesis, we sampled invertebrate communities and physicochemical conditions from 168 streams within the mountaintop removal-valley fill mining region of West Virginia. We used redundancy analysis to first test for significant effects of local (observed physicochemical conditions) and neighborhood (streams within a 5 km buffer) degradation on assemblage structure across all taxa and stress tolerance (low, moderate, high) and dispersal (low, high) categories. We then used generalized linear and hurdle models to characterize changes in community metrics and individual taxa, respectively. Local condition consistently explained the majority of variation (partial R^2 up to 5× those of neighborhood condition) in community structure and was the only factor affecting sensitive taxa. Neighborhood condition explained significant variation in moderately tolerant taxa with low dispersal capacity and highly tolerant taxa, regardless of dispersal. Decreased occurrence (*Baetis*) and abundance (*Maccaffertium*) of key taxa and corresponding metrics (%E, %EPT) suggest decreased dispersal and associated mass and rescue effects within degraded neighborhoods. Decreased neighborhood conditions also resulted in the proliferation of tolerant taxa (Chironomidae, *Chimarra*, *Hemerodromia*). Our results suggest communities within even the most pristine streams are at risk when isolated within heavily impacted regions. Consequently, protection of regional species' pools in heavily impacted regions will require more than simply conserving un-impacted streams.

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1. Introduction

Advances in metacommunity ecology have led to an emerging paradigm recognizing the importance of regional factors (e.g., species pool and location within dispersal networks) and processes (e.g., dispersal and mass effects) in structuring local assemblages (Heino et al., 2003; Leibold et al., 2004; Brown and Swan, 2010; Hitt and Angermeier, 2011). An important avenue of continued research concerns applying metacommunity theory to the management of disturbed ecosystems (Brown et al., 2011; Heino, 2013). For example, preservation of undisturbed headwater catchments has become an important component of freshwater conservation efforts within actively developing watersheds (Lowe and Likens, 2005). A major motivation for their preservation is the understanding that headwater streams contribute disproportionately to regional biodiversity and serve as critical habitat for the preservation of regionally rare and endangered taxa (Lowe and Likens, 2005; Meyer et al., 2007; Finn et al., 2011).

However, extensive local disturbances occurring across larger spatial scales have the potential to alter communities within undisturbed streams through disruption of regional metapopulation and metacommunity structure and processes. Increasing isolation of intact tributaries through expanding human activity may result in dispersal limitation and decreased mass and rescue effects (i.e., dispersal of a taxa from suitable habitats to suboptimal or extirpated habitats), particularly for regionally sensitive taxa and/or taxa with low dispersal ability (Astorga et al., 2012; Vanschoenwinkel et al., 2013; Radkova et al., 2014; Heino et al., 2015). Moreover, extensive disturbance may also facilitate establishment and proliferation of subdominant competitors and disturbance tolerant specialists via mass effects from degraded surrounding streams (Pandit et al., 2009; Vanschoenwinkel et al., 2013). Consequently, the ability of intact communities to preserve regional biodiversity may be limited as they become increasingly isolated within heavily impacted systems (Campbell and McIntosh, 2013; Heino, 2013). To our knowledge, however, this has never been demonstrated.

We provide such an assessment by analyzing macroinvertebrate communities from the central Appalachian region in relation to their influence from local and regional (i.e., neighborhood, *sensu* Merovich et al., 2013) drivers of environmental degradation. We focus on the primary mountaintop removal-valley fill (MTR-VF) mining region because stream networks within this region offer a relevant opportunity to demonstrate regional metacommunity processes in an actively developing landscape with important current and future socioeconomic implications. Extensive contemporary and historic coal mining and residential development activities within this region have resulted in widespread ecological impacts (Bernhardt et al., 2012; Merriam et al., 2015a, 2015b). However, the geography of land use activities within this region creates a unique juxtaposition of severely degraded streams within otherwise pristine stream networks and high quality streams within otherwise severely degraded networks (Merovich et al., 2013). Consequently, we had the rare opportunity to collect an un-confounded dataset with respect to local and regional controls over community composition across a large spatial scale (see Ewers and Didham, 2006).

Previous efforts to quantify spatial constraints over community structure and processes (i.e., dispersal) have used spatial location and distance among sites to represent spatial structuring. However, inferences regarding the importance of metacommunity processes (i.e., mass effects and dispersal) from such studies are limited by the spatial extent encompassing the sampling sites (Heino et al., 2015). Herein, we constructed an index of neighborhood condition that describes the extent to which each study site is isolated by surrounding land use activity and aquatic degradation (*sensu* Merovich et al., 2013). Consequently, we were able to directly test the hypothesis that both local physicochemical conditions and the degree of isolation (i.e., neighborhood condition) significantly influence local community composition. We further hypothesized that the effects of isolation are mediated by tolerance and dispersal characteristics. More specifically, we expect increasing isolation will have a strong negative effect on sensitive taxa with low dispersal abilities owing to decreased mass and rescue effects. We further expect that increasing isolation will have a strong positive effect on tolerant taxa, regardless of dispersal capacity, via increased mass effects from nearby degraded streams. It is important to note that our use of the term 'isolation' refers to the extent to which a site is surrounded by degraded aquatic conditions and does not imply jurisdiction under the Clean Water Act.

2. Materials and methods

2.1. Study area and site selection

The study region is comprised of the eight 8-digit hydrologic unit code watersheds intersecting the mountaintop mining region within West Virginia (Fig. 1). These watersheds drain approximately 20,795 km^2 and include the Tug Fork, Twelvepole Creek, and Elk, Gauley, Upper Kanawha, Upper and Lower Guyandotte, and Coal Rivers. We selected 168 streams as study sites (Fig. 1). Sites were selected to be evenly distributed across drainage basins and to represent the full gradient of combined local and network (neighborhood) conditions [i.e., streams with high and low quality local conditions located within intact and degraded stream networks]. All study sites had basin areas <40 km^2 and were independent of one another with respect to upstream-to-downstream flow (Petty et al., 2010).

2.2. Local physicochemical condition

We sampled physicochemical attributes once at each site during the summers (July–August) of 2010, 2011, or 2012. A detailed description of our physicochemical sampling protocol is provided by Merriam et al. (2015a). Briefly, reaches were defined as 40× mean stream width, with minimum and maximum reach lengths of 150 and 300 m. We measured overall habitat quality with US Environmental Protection Agency (EPA) rapid visual habitat assessments (RVHA; Barbour et al., 1999). We obtained in-situ measures of specific conductance, dissolved oxygen, pH, and temperature. We obtained filtered samples for determination of dissolved Al, Ba, Ca, Cd, Cr, Fe, K, Mg, Mn, Na, Ni, Se, and Zn and unfiltered samples for determination of NO_3, NO_2, total P, alkalinity, Cl, SO_4, and total dissolved solids. The current study uses previously described chemical signatures (i.e., principal components) to describe patterns in local chemical conditions related to contemporary surface mining [Ca^{2+}, K^+, Mg^{2+}, SO_4^{2-}, and HCO_3^-, and Se; henceforth referred to as mining water quality (mWQ)] and residential development [Na^+, Cl^-, and Ba; residential water quality (rWQ)] – the dominant land use activities within the study region (Merriam et al., 2015b).

2.3. Macroinvertebrate community data

We sampled benthic macroinvertebrate communities immediately following physicochemical sampling with procedures established by the West Virginia Department of Environmental Protection (WV DEP) Watershed Assessment Program (WV DEP, 2009). We obtained kick samples (net dimensions 335 × 508 mm with 500-μm mesh) from 4 targeted riffles distributed throughout the reach and combined organisms and debris into a single composite sample for each site. Samples were immediately preserved with 95% ethanol. In the laboratory, we sub-sampled macroinvertebrate communities following the 200 count method (WV DEP, 2009). We identified organisms to genus, except Mollusca (family), Chironomidae, Hydracarina, Oligochaeta, and Nematoda, with keys in Merritt and Cummins (2008).

We categorized taxa based on WV DEP-defined tolerance values that reflect relative sensitivity to anthropogenic influence [low (0–2), moderate (3–5), and high (6–10)]. We categorized taxa with respect to dispersal capacity (high, low) using 2 traits characterizing adult dispersal

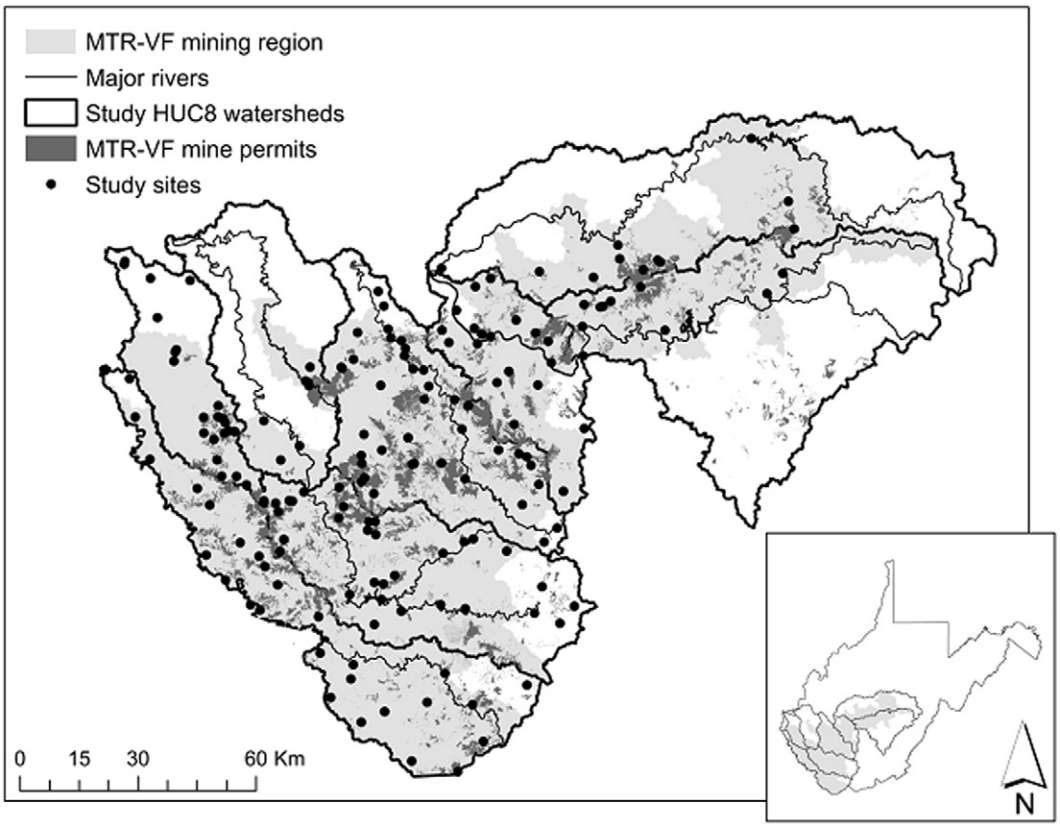

Fig. 1. Map of target 8-digit hydrologic unit code (HUC) watersheds intersecting the primary mountaintop removal-valley fill (MTR-VF) region within West Virginia. Major rivers, surface mine permits, and study sites are shown.

[female dispersal distance (high or low) and flying strength (high or low)] from a published database (Poff et al., 2006). Taxa were considered to have high dispersal capacity if they fell within the 'high' category for either dispersal trait. We obtained tolerance and dispersal characteristics for 84 taxa comprising 92% of all individuals. Trait data are presented in S1.

Abundance data were used to calculate community metrics. We calculated family-level (WVSCI; Gerritsen et al., 2000) and genus-level (GLIMPSS (CF); Pond et al., 2013) multi-metric indices developed for West Virginia. Both WVSCI and GLIMPSS (CF) score streams on a scale of 0–100. We calculated 7 additional metrics shown to be responsive to stressors throughout the study region: total genus richness, Ephemeroptera, Plecoptera, Trichoptera (EPT) richness, E richness, P richness, % EPT, %E, and %Chironomidae (Pond et al., 2008; Merriam et al., 2011).

2.4. Neighborhood condition

We created an index of neighborhood condition characterizing physicochemical degradation within a 5 km zone centered on each study site. Previous efforts have demonstrated 5 km to be the most appropriate distance when quantifying effects of surrounding streams and the associated species pool on local assemblage structure (Sundermann et al., 2011). To do this, we followed procedures outlined in Merovich et al. (2013) to summarize predicted local (1:24:000 stream segments) conditions at the neighborhood-scale (5 km zone) via a 3-step process.

2.4.1. Predicting local conditions

First, we constructed boosted regression tree (BRT) models relating mWQ and rWQ to land cover and use characteristics and used these models to predict mWQ and rWQ for the entire study region (see S2 for a detailed discussion of landscape characteristics, BRT models, and model results). Predicted mWQ and rWQ values were scaled to range between 0 and 100, relative to the best and worst regional values, respectively.

2.4.2. Weighting local conditions

We then weighted scaled predictions to account for unequal effects of mWQ and rWQ on local assemblage structure. We used partial redundancy analysis [RDA; rda () function in package *vegan*] to estimate the variation in community composition explained by observed mWQ and rWQ (Legendre and Legendre, 2012). RDA was run on taxa for which we had both tolerance and dispersal information (n = 84). Abundance data were Hellinger-transformed to meet assumptions of linear ordination techniques (Peres-Neto et al., 2006). We spatially detrended transformed abundances [RDA(abundances ~ X + Y)] and ran final RDA models on resulting residuals to account for spatial trends that may confound environmental effects. We used adjusted R^2, which provides unbiased estimates of variance (Peres-Neto et al., 2006), as final weights for mWQ ($pR^2 = 0.05$; $p < 0.01$) and rWQ ($pR^2 = 0.03$; $p < 0.01$).

2.4.3. Scaling conditions

Finally, we summarized predicted local (i.e., stream segment) conditions at the neighborhood (i.e., 5 km zone) scale. We multiplied weighted mWQ and rWQ scores by local stream segment length, summed each value across all segments in a given neighborhood, and standardized by total neighborhood stream length. This resulted in scaled mWQ and rWQ values for each neighborhood, which were summed to create a combined index of neighborhood condition (cNCI) for each site. cNCI values were √x-transformed to approximate normality.

2.5. Statistical analyses

2.5.1. Hypothesis 1: local conditions and isolation influence local community composition

We used RDA to quantify the relative contributions of local (RVHA, mWQ, rWQ) and neighborhood (cNCI) environmental matrices to Hellinger-transformed and spatially detrended abundance data across all taxa (n = 84). Given a significant global model, we ran a forward selection procedure ($p < 0.1$ for inclusion) to retain only the most important predictors (i.e., local only, neighborhood only, or their combination). When both local and neighborhood conditions were significant, we used partial RDA to estimate the total variation in community composition explained by each component. We report adjusted R^2 to provide unbiased estimates of variance (Peres-Neto et al., 2006).

We then used generalized linear models (GLM) within an information theoretic framework to test for local and neighborhood effects on community metrics. Each metric was spatially detrended [glm(metric ~ X + Y)] and final models were run on resulting residuals. We created 4 candidate models for each metric testing for local-only effects, neighborhood-only effects (i.e., cNCI), a combination of local and neighborhood effects (i.e., local + cNCI), and a null model. Local effects (mWQ, rWQ, RVHA) are expected to vary among response variables. Thus, we applied a backward deletion [deletion tests (likelihood ratio tests; $\alpha = 0.10$)] to remove unimportant local variables from each candidate set prior to model comparison [lrtest () function in package *lmtest*] (Crawley, 2005). We used Akaike's information-criterion corrected for small sample size (AIC_c) to compare candidate models. We compared candidate models using ΔAIC_c and Akaike weights (w_i) [function model.sel in package *MuMIN*]. We assessed multicollinearity among covariates using the variance inflation factor (VIF) statistic [function vif() in package *DAAG*]. All covariates had VIF <2. Covariates were centered and scaled to enable comparison of effect strength. We present all models with $\Delta AIC < 2$, but make inferences based on the best candidate model in each set (Burnham and Anderson, 2002).

2.5.2. Hypothesis 2: effects of isolation are mediated by tolerance and dispersal characteristics

To test whether isolation differentially affected organisms based on tolerance and dispersal characteristics, we ran RDA separately on taxa falling within each tolerance (low, moderate, high) and dispersal (low, high) category, as well as on each tolerance and dispersal combination. We followed previously described methods for RDA.

To more thoroughly characterize the strength and pattern of isolation effects, we created regression models for 9 taxa. We selected 7 taxa previously shown to be responsive to regional stressors [3 Ephemeroptera (*Baetis*, *Maccaffertium*, *Caenis*) and 4 Trichoptera (*Chimarra*, *Rhyacophila*, *Ceratopsyche*, and *Cheumatopsyche*) genera] (Pond et al., 2008; Pond, 2010, 2012). We also modeled 2 dominant Diptera (Chironomidae and *Hemerodromia*). With the exception of Chironomidae, we used hurdle count regression models to account for zero-inflation in taxon abundances [function hurdle() in package *pscl*]. Hurdle models combine a binomial probability component (binomial distribution with a logit link) that predicts occurrence and a zero-truncated component (negative binomial distribution with a logit link) that models positive counts (Zeileis et al., 2008). Chironomidae was modeled using GLM with a negative binomial distribution. The same 4 candidate models were constructed for each taxon (local-only, neighborhood-only, local and neighborhood, and null). However, we included separate models testing for neighborhood effects on occurrence, abundance, and their combination for hurdle models. Spatial location (X and Y coordinates) was included in initial models and subjected to deletion tests along with local predictors. Significant spatial effects were included in subsequent models to account for spatial trends while maintaining data distributions required for hurdle models. We used the best candidate model in each set to predict taxonomic response to cNCI under optimal (i.e., best observed), average, and worst conditions for all local covariates.

3. Results

3.1. Hypothesis 1: local conditions and isolation influence local community composition

RDA models obtained by forward selection indicated that both local and neighborhood conditions explained significant variation in community composition across all taxa (n = 84) (Fig. 2A). The best models (i.e., lowest AIC_c) for 4 of 9 community metrics included both local and neighborhood condition factors (Table 1). cNCI had a negative effect on %E and %EPT and a positive effect on total genus richness and % Chironomidae (Table 2). However, effects of local physicochemical conditions were consistently stronger (1.8 to 2.9×) than those of cNCI. The best models for GLIMPSS, WVSCI, EPT richness, E richness, and P richness included only local environmental factors (Tables 1, 2).

3.2. Hypothesis 2: effects of isolation are mediated by tolerance and dispersal characteristics

The strength of local and neighborhood effects varied among tolerance and dispersal categories. When considering tolerance independent of dispersal capacity, both local and neighborhood factors were significantly associated with taxa having moderate and high tolerance values

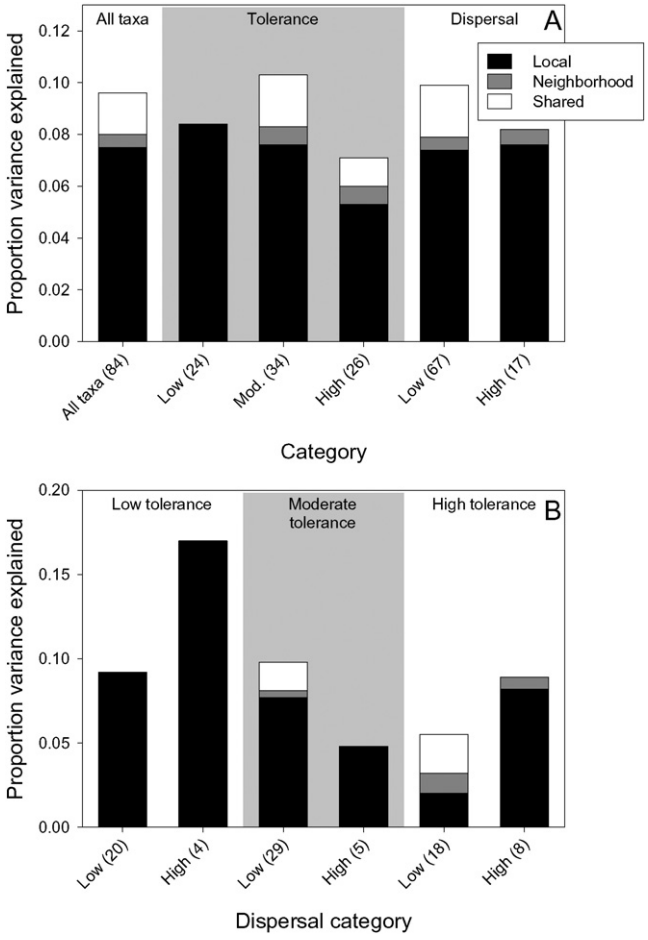

Fig. 2. Proportion of community data explained (i.e., adjusted partial R^2) by local (mWQ, rWQ, and RVHA scores) and neighborhood (cNCI) conditions as calculated by redundancy analysis (RDA). Results are presented for all taxa and separately for the 3 tolerance (low, moderate, and high) and 2 dispersal (low and high) categories (A). We also present results run on each of the 6 unique combinations of tolerance and dispersal capacity (B).

Table 1
Model selection metrics for generalized linear models relating spatially detrended community metrics to local and neighborhood conditions. Models with ΔAIC <2 are presented. m = mining; r = residential; c = combined; WQ = water quality; RVHA = rapid visual habitat assessment score; NCI = neighborhood condition index; E = Ephemeroptera; P = Plecoptera; T = Trichoptera; Chiron = Chironomidae; rich = richness; GLIMPSS = Genus Level Index of Most Probable Stream Status; WVSCI = West Virginia Stream Condition Index.

Metric	Model	AIC_c	ΔAIC	w_i
GLIMPSS[a]	mWQ + rWQ + RVHA	−167.6	0.00	0.742
WVSCI	mWQ + rWQ + RVHA	1294.2	0.00	0.700
	mWQ + rWQ + RVHA + cNCI	1295.9	1.69	0.300
Genus rich	mWQ + rWQ + cNCI	−11.0	0.00	0.702
	mWQ + rWQ	−9.3	1.71	0.298
EPT rich	mWQ + rWQ + RVHA	159.8	0.00	0.736
E rich	mWQ	346.0	0.00	0.738
P rich	mWQ + rWQ	507.3	0.00	0.737
% EPT[a]	rWQ + RVHA + cNCI	−21.1	0.00	0.595
	rWQ + RVHA	−20.4	0.77	0.405
% E[a]	mWQ + cNCI	−67.1	0.00	0.859
% Chiron[b]	mWQ + rWQ + cNCI	658.7	0.00	0.580
	mWQ + rWQ	659.4	0.65	0.419

[a] arcsine√x-transformed.
[b] √x-transformed.

(Fig. 2A). Only local environmental conditions were retained for organisms with low tolerance. Both low and high dispersing organisms were significantly influenced by local and neighborhood factors, independent of tolerance (Fig. 2A). When simultaneously considering tolerance and dispersal, both local and neighborhood factors were retained by forward selection and explained significant variation in moderately tolerant, low dispersing organisms. Both local and neighborhood factors explained significant variation in organisms with high tolerance and low and high dispersal capacities (Fig. 2B). Only local environmental factors were retained for organisms with low tolerance, regardless of dispersal capacity (Fig. 2B). Only local factors were retained for moderately tolerant, high dispersing organisms.

The best models for 5 of 9 taxa included both local and neighborhood effects (Table 3). Combined NCI was associated with decreased occurrence of *Baetis* and *Ceratopsyche* and decreased abundance of *Maccaffertium*. In contrast, cNCI had a positive effect on the occurrence of *Chimarra* and abundance of Chironomidae (Table 4). However, the effects of local conditions tended to be much stronger (1.5–2.2×) than those of cNCI (Table 4). cNCI was associated with increased occurrence and abundance of *Hemerodromia* in the absence of any local effect (Tables 3, 4). Spatial location was included along with cNCI in the final models for *Ceratopsyche*, *Hemerodromia*, and Chironomidae (Table 4).

Table 2
Scaled parameter estimates (and standard errors) for best approximating models (i.e., lowest AIC_c) relating detrended [glm(metric ~ X + Y)] community metrics to local and neighborhood conditions. WQ = water quality; RVHA = rapid visual habitat assessment score; cNCI = combined neighborhood condition index; E = Ephemeroptera; P = Plecoptera; T = Trichoptera; GLIMPSS = Genus Level Index of Most Probable Stream Status; WVSCI = West Virginia Stream Condition Index.

Metric	mWQ	rWQ	RVHA	cNCI
GLIMPSS[a,d]	−6.6 (1.2)	−8.1 (1.2)	2.5 (1.2)	–
WVSCI	−3.8 (0.9)	−5.3 (0.9)	1.7 (0.9)	–
Genus richness[d]	−11.5 (2.0)	−9.9 (1.8)	–	4.0 (2.1)
EPT richness[c]	−2.1 (0.3)	−1.5 (0.3)	0.6 (0.3)	–
E richness[c]	−5.0 (0.5)	–	–	–
P richness[c]	−5.6 (0.8)	−5.3 (0.8)	–	–
% EPT[a,d]	–	−4.4 (1.8)	5.4 (1.8)	−3.0 (1.7)
% E[a,d]	−8.5 (2.0)	–	–	−4.1 (2.0)
% Chironomidae[b,c]	−3.89 (1.5)	4.41 (1.3)	–	2.5 (1.5)

[a] arcsine√x-transformed.
[b] √x-transformed.
[c] Values presented as 1×10^{-1}.
[d] Values presented as 1×10^{-2}.

Table 3
Model selection metrics for hurdle models relating probability of occurrence and abundance of selected taxa to local and neighborhood conditions. Models with ΔAIC <2 are presented. m = mining; r = residential; c = combined; WQ = water quality; RVHA = rapid visual habitat assessment score; NCI = neighborhood condition index; XY = latitude and longitude.

Taxon	Model structure	AIC_c	ΔAIC	w_i
Moderate tolerance, low dispersal				
Maccaffertium	$mWQ^{a,b} + cNCI^{b}$	573.6	0.00	0.618
	$mWQ^{a,b} + cNCI^{a,b}$	574.9	1.32	0.320
Chimarra	$mWQ^{a,b} + RVHA^{a,b} + cNCI^{a}$	459.6	0.00	0.436
	$mWQ^{a,b} + RVHA^{a,b} + cNCI^{a,b}$	459.8	0.24	0.388
Rhyacophila	$mWQ^{a,b} + rWQ^{a} + RVHA^{b} + Y^{a}$	184.5	0.00	0.555
High tolerance, low dispersal				
Baetis	$mWQ^{a} + RVHA^{b} + cNCI^{a}$	1142.6	0.00	0.334
	$mWQ^{a} + RVHA^{b}$	1143.4	0.75	0.230
	$mWQ^{a} + RVHA^{b} + cNCI^{a,b}$	1143.5	0.86	0.217
	$mWQ^{a} + RVHA^{b} + cNCI^{b}$	1143.5	0.86	0.217
Caenis	$rWQ^{a} + X^{a,b} + Y^{b}$	234.7	0.00	0.402
	$rWQ^{a} + X^{a,b} + Y^{b} + cNCI^{b}$	235.3	0.63	0.294
	$rWQ^{a} + X^{a,b} + Y^{b} + cNCI^{a}$	236.6	1.91	0.155
Hemerodromia	$X^{b} + Y^{b} + cNCI^{a,b}$	964.4	0.00	0.447
	$mWQ^{a,b} + rWQ^{a} + X^{b} + Y^{b} + cNCI^{b}$	965.4	0.98	0.274
	$mWQ^{a,b} + rWQ^{a} + X^{b} + Y^{b} + cNCI^{a,b}$	965.5	1.14	0.253
High tolerance, high dispersal				
Ceratopsyche	$mWQ^{a,b} + rWQ^{a,b} + RVHA^{b} + X^{a,b} + Y^{a,b} + cNCI^{a}$	967.6	0.00	0.487
	$mWQ^{a,b} + rWQ^{a,b} + RVHA^{b} + X^{a,b} + Y^{a,b} + cNCI^{a,b}$	969.1	1.56	0.224
Cheumatopsyche	$RVHA^{a} + X^{a} + Y^{b}$	1423.4	0.00	0.362
	$RVHA^{a} + X^{a} + Y^{b} + cNCI^{a}$	1424.5	1.03	0.216
Chironomidae	mWQ + rWQ + cNCI	1621.2	0.00	0.683
	mWQ + rWQ	1622.8	1.53	0.317

[a] Variables included in the probability of occurrence model component.
[b] Variables included in the abundance model component.

The best models for *Rhyacophila*, *Caenis*, and *Cheumatopsyche* included only local and spatial effects.

Predicting occurrence and abundance for selected taxa illustrates differential response to the combined effects of local and neighborhood conditions (Fig. 3). The occurrence of *Chimarra* was predicted to increase with increasing cNCI, and it was predicted to be higher at a given cNCI when local conditions were good (Fig. 3A). *Baetis* and *Ceratopsyche* occurrences were predicted to decrease with increasing cNCI; however, *Baetis* occurrence was predicted to be higher at a given cNCI when local conditions were good, while *Ceratopsyche* occurrence was predicted to be higher when local conditions were poor (Fig. 3B, C). *Maccaffertium* abundance was predicted to be very low in both average and poor local conditions, regardless of cNCI (Fig. 3D). *Maccaffertium* abundance in streams with good local conditions was strongly influenced by cNCI. The abundance of *Hemerodromia* was predicted to increase with increasing cNCI independent of local conditions (Fig. 3E). In contrast, Chironomidae abundance was predicted to increase with both decreasing cNCI and decreasing local condition (Fig. 3F).

4. Discussion

Pervasive land use development appears to degrade macroinvertebrate communities via two distinct and significant pathways: 1 - degradation of local physicochemical conditions, and 2 - increasing isolation via degradation of surroundings streams. In the current study, local habitat consistently explained the most variance in local community composition (i.e., pR^2 up to 5× those of cNCI values), supporting the general tenet that local physicochemical conditions represent the dominant control over macroinvertebrate assemblage structure. However, isolation via neighborhood degradation appears to further impact local communities via apparent alterations to important metacommunity processes. More specifically, we observed significant negative effects

Table 4
Scaled parameter estimates (and standard errors) for hurdle models relating probability of occurrence and abundance of selected macroinvertebrate taxa to local and neighborhood conditions. m = mining; r = residential; c = combined; WQ = water quality; RVHA = rapid visual habitat assessment score; NCI = neighborhood condition index; XY = latitude and longitude.

	mWQ	rWQ	RVHA	cNCI	X	Y
Probability of occurrence component						
Moderate tolerance, low dispersal						
Maccaffertium	−1.53 (0.25)	–	–	–	–	–
Chimarra	0.34 (0.22)	–	0.68 (0.21)	0.50 (0.22)	–	–
Rhyacophila	−0.45 (0.23)	−1.21 (0.33)	–	–	–	0.45 (0.28)
High tolerance, low dispersal						
Baetis	−0.78 (0.24)	–	–	−0.37 (0.22)	–	–
Caenis	–	0.66 (0.23)	–	–	−0.82 (0.27)	–
Hemerodromia	–	–	–	0.67 (0.24)	–	–
High tolerance, high dispersal						
Ceratopsyche	0.59 (0.21)	−0.36 (0.18)	–	−0.39 (0.21)	0.38 (0.18)	−0.34 (0.19)
Cheumatopsyche	–	–	0.54 (0.29)	–	−0.61 (0.31)	–
Chironomidae	NA	NA	NA	NA	NA	NA
Abundance component						
Moderate tolerance, low dispersal						
Maccaffertium	−0.98 (0.22)	–	–	−0.45 (0.17)	–	–
Chimarra	0.54 (0.30)	–	0.84 (0.41)	–	–	–
Rhyacophila	−0.86 (0.39)	–	1.17 (0.77)	–	–	–
High tolerance, low dispersal						
Baetis	–	–	−0.32 (0.14)	–	–	–
Caenis	–	–	–	–	−0.49 (0.29)	−0.43 (0.19)
Hemerodromia	–	–	–	0.36 (0.09)	−0.33 (0.09)	0.11 (0.10)
High tolerance, high dispersal						
Ceratopsyche	0.55 (0.13)	−0.33 (0.15)	0.27 (0.13)	–	0.30 (0.16)	−0.72 (0.16)
Cheumatopsyche	–	–	–	–	–	−0.14 (0.08)
Chironomidae	−0.18 (0.06)	0.19 (0.05)	–	0.13 (0.06)	−0.14 (0.05)	–

of increasing isolation on poor dispersing and moderately sensitive taxa and positive effects on highly tolerant taxa. These findings have important implications regarding the management of aquatic resources and suggest communities within even the most pristine streams are threatened when isolated within heavily impacted regions.

These results generally support our initial hypotheses regarding the role of tolerance and dispersal in mediating effects of isolation on community composition. We expected that degraded neighborhood conditions would result in regional expansion and proliferation of tolerant taxa. RDA found significant effects of cNCI on tolerant organisms regardless of dispersal ability, and linear models suggested increased occurrence and abundance of several highly (Chironomidae, *Hemerodromia*) and moderately (*Chimarra*) tolerant taxa with decreasing neighborhood condition (i.e., increasing isolation). Thus, increasing isolation appears to alter local communities through increased immigration of tolerant taxa from highly stressed neighboring streams.

We also expected to see strong negative effects of degraded neighborhood condition on sensitive, poor dispersing taxa. However, we failed to observe significant associations between cNCI and the most sensitive taxa, regardless of dispersal ability. We did, however, observe significant effects of cNCI across moderately tolerant taxa with low dispersal capacity, as well as decreases in %E and %EPT and in the probability of occurrence and abundance of associated taxa (e.g., *Baetis* and *Maccaffertium*) previously shown to be sensitive to regional stressors [i.e., mining-related water chemistry (Pond, 2010; Pond, 2012)]. Thus, increasing isolation within impacted neighborhood appears to limit dispersal and associated mass and rescue effects of certain moderately tolerant taxa. In contrast, sensitive taxa may represent habitat specialists that are able to out-compete expanding tolerant taxa and avoid extirpation in the face of neighborhood degradation. It is also possible that degraded neighborhood condition results in the loss of sensitive taxa over timeframes not captured by the current study. Communities within impacted ecosystems often experience greater extinction rates as individual taxa reach new equilibria corresponding to current landscape (or riverscape) structure (Hanski and Ovaskainen, 2002). This 'extinction debt' often occurs over long timeframes, particularly at large spatial scales (Hanski and Ovaskainen, 2002; Vellend et al., 2006; Dullinger et al., 2013).

To our knowledge, ours is the first study to demonstrate the importance of both organism tolerance and dispersal capacity in structuring invertebrate metacommunities within human-dominated landscapes, despite recent calls for such studies (Heino, 2013). In fact, few studies quantifying processes governing metacommunity structure have been conducted within heavily degraded systems (but see Kitto et al., 2015; Smith et al., 2015). Nevertheless, recent studies have begun to demonstrate the importance of taxonomic characteristics in structuring natural metacommunities. Our results corroborate previous work documenting differential effects of regional and spatial factors on organisms with varying dispersal capabilities (Astorga et al., 2012; Canedo-Arguelles et al., 2015; Smith et al., 2015), as well as significant effects of isolation on community structure (Campbell and McIntosh, 2013; Radkova et al., 2014). Previous studies have also documented an increase in habitat generalists in systems affected by natural disturbance (Vanschoenwinkel et al., 2013), while habitat specialists have been shown to respond solely to local conditions (Pandit et al., 2009; Radkova et al., 2014). It is important to note, however, that our analyses were based on genus-level identifications and organism traits. This represents a potential limitation because congeners often exhibit differential sensitivities to stressors, potentially affecting or biasing observed relationships. Thus, we recommend further investigation using species-level data.

Our study also adds to a growing body literature demonstrating the importance of multi-scale and metacommunity processes in shaping local community composition in aquatic ecosystems (see Heino et al., 2003; Sanderson et al., 2005; Brown et al., 2011; Heino, 2013; Stoll et al., 2016). However, ours is the first study to demonstrate regional control over local community composition within the MTR-VF region. Thus, it represents an important step toward the successful management of aquatic resources within this dynamic region. Management efforts within the MTR-VF region have focused on constructing models for predicting biological impairment from current and future land use activities (Merriam et al., 2013, 2015a; Petty et al., 2013). Neighborhood

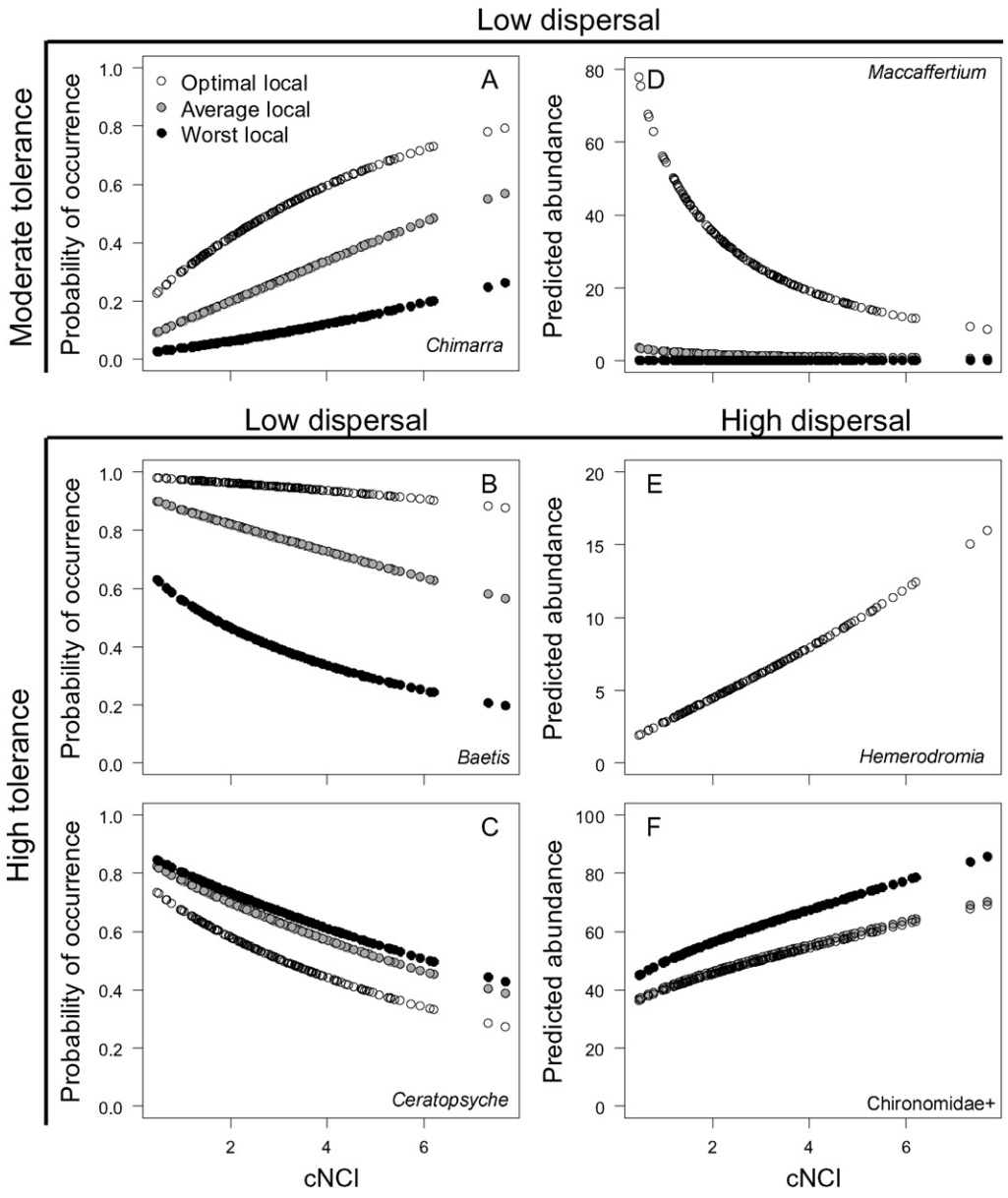

Fig. 3. Probability of occurrence and abundance of selected taxa as a function of cNCI given optimal (i.e., best observed), average, and worst observed conditions for all local covariates (mWQ, rWQ, and RVHA scores). Taxa are shown with respect to tolerance and dispersal categories.

condition did not contribute to community degradation as quantified by either index of biotic integrity currently used by West Virginia to designate impairment (i.e., WVSCI and GLIMPSS). Previous evidence suggests metacommunity dynamics are often inherently imbedded within watershed-scale models of biological condition (Mykra et al., 2007; Heino et al., 2012). Thus, the current results do not suggest that previously constructed models inaccurately predict impairment. However, we caution that managing based solely on landscape attributes risks overgeneralizing the relative importance of neighborhood condition and its effects on community structure, potentially resulting in suboptimal regulatory decisions.

Our study is unique in that we used an index of surrounding aquatic resource degradation to test for spatial effects on community composition. This technique is in contrast to more common approaches that use geographic location to define spatial structuring across study sites (e.g., spatial eigenfunction analysis). However, unlike these other approaches, our inferences regarding the importance of metacommunity processes (i.e., dispersal and mass effects) are not influenced by distances between sites and geographic extent surveyed (see Heino et al., 2015). In fact, we quantified significant effects of degraded neighborhood condition on macroinvertebrate communities independent of purely spatial (i.e., geographic coordinates) trends in assemblage structure. This enabled us to provide unbiased estimates of neighborhood effect strength with respect to spatial autocorrelation in community structure. It is possible, however, that significant linear trends represent metacommunity processes occurring at larger spatial scales or effects of degraded neighborhood conditions associated with spatial patterns in land use development. Consequently, our estimates of neighborhood effect strength may underrepresent the actual importance of regional (metacommunity) processes in structuring local assemblages.

Nevertheless, there are several potential limitations associated with our measure of neighborhood condition. First, our approach assumes the index of neighborhood condition, which is derived from predicted habitat quality, accurately reflects the surrounding metacommunity and associated species pool. Stoll et al. (2016) utilized a similar approach and demonstrated a significant effect of continuously measured

habitat quality in surrounding streams (i.e., 5 km zone) on local community composition. Although we used predicted measures of surrounding habitat, BRT was able model chemical conditions with a high degree of certainty and accuracy, and model results corroborated previous efforts to characterize chemical degradation throughout the study region (Merriam et al., 2015b). It is important to also note that our measures of neighborhood condition and subsequent analyses focus on aerial dispersal and do not explicitly consider within-network distance or dispersal via drift (Brown et al., 2011). However, recent research has shown little difference between overland and within-network distance measures when characterizing metacommunity structuring and predicting colonization (Gronroos et al., 2013; Tonkin et al., 2014), highlighting the importance of overland dispersal in structuring metacommunities in fragmented landscapes (Didham et al., 2012). Thus, we are confident in the validity of our methodology and associated results.

5. Conclusions and recommendations for resource managers

The current results underscore previous calls for more holistic approaches to aquatic resource management that address conditions and processes at hierarchical spatial scales (Petty and Thorne, 2005; Palmer, 2009; Merovich et al., 2013). For example, previous research suggests restoration efforts should focus on impacted streams within relatively un-impacted neighborhoods because of ecological benefits associated with having good streams nearby (i.e., increased species pool and dispersal potential) (McClurg et al., 2007; Sundermann et al., 2011; Tonkin et al., 2014). Moreover, Stoll et al. (2016) suggest the success of reach-scale restoration efforts will be greatest when located within regions with intermediate habitat quality. Our results further suggest that reach-scale restoration and watershed management efforts should maximize improvement of neighborhood condition in an effort to maintain metacommunity processes.

Perhaps most importantly, our study suggests that the preservation of individual headwater catchments [i.e., designating them as protected areas, conservation priorities, or critical management zones (Meyer et al., 2007)] may not be sufficient to maintain regional diversity and integrity within this and other actively developing or highly altered landscapes. Moreover, degraded regional conditions likely influence the functional capacity of undisturbed communities, particularly with respect to food webs and associated trophic linkages (see Meyer et al., 2007; Lowe and Likens, 2005). It is important to note, however, that our study does not consider benefits of undisturbed streams related to water quality, hydrology, and linkages to terrestrial systems (Lowe and Likens, 2005). Such benefits are further justification for the preservation of isolated headwater streams, particularly within heavily impacted regions.

Continued aquatic resource degradation under current land use development trends within the MTR-VF region of West Virginia may result in irreparable impacts to macroinvertebrate communities owing to the disruption of important metacommunity processes. Resource managers will need to have important discussions regarding realistic goals and expectations of regulatory (e.g., permitting) and management (e.g., protection and restoration) decisions in the face of continued land use development within this dynamic and globally important energy-producing landscape. We hope the results provided herein will provide an important starting point for such discussions. Perhaps more importantly, however, the results of this study should be extended to all ecosystem types within other actively developing landscapes in order to appropriately manage landscapes and ensure resource sustainability.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2016.04.053.

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